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# BIOLOGICAL BULLETIN.

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## AN AMERICAN CERAPACHYS, WITH REMARKS ON THE AFFINITIES OF THE CERAPACHYINÆ.<sup>1</sup>

WILLIAM MORTON WHEELER.

The singular ant described in the following pages was discovered by Miss Augusta Rucker within the city limits of Austin, Texas, on May 11 of the current year. Impressed by the peculiar, elongate, and segmentally constricted body of the insect, Miss Rucker fortunately secured nearly all the individuals in the nest, including the apterous queen. The most superficial study showed that the insect could belong to none of the described North or South American genera of Formicidæ. A note from Professor Emery, to whom a few of the specimens were sent, and comparison with some rare ants generously sent me by that gentleman and by Dr. Gustav Mayr, made it perfectly evident that the new form must be assigned to the interesting genus *Cerapachys* (subgenus *Parasyscia*), representatives of which were hitherto known only from the Old World (Africa, Asia and Papuasia).

The *Cerapachys* nest was found about six inches below the surface soil under a layer of large flakes of limestone in the shade of some hackberry trees growing on the banks of Waller Creek. At first only six workers and the queen were taken, but on the following day Miss Rucker and myself succeeded in unearthing four more workers on the same spot. The whole nest could not have contained much more than a dozen specimens. Unfortunately there were no larvæ or pupæ. When first seen the *Cerapachys* were engaged in a battle with some much smaller subterranean ants (*Ponera trigona* var. *opacior*) which seemed to be invading the nest. The new species was slow in its move-

<sup>1</sup> Contributions from the Zoölogical Laboratory of the University of Texas, No. 37.

ments as would be expected in creatures with such long bodies and short legs. They did not "feign death" when roughly handled, though some of them, when held in the forceps, remained motionless in the attitude probably assumed when they are being deported by their sister workers. While creeping about the ants carried their very robust antennæ in a peculiar manner. The scape was held erect or inclined forwards, but hardly in a horizontal or lateral position as in other ants, while the funicle could be folded down onto the front surface of the scape a little obliquely to the side. The habits, so far as these could be inferred from the little I saw of the ants in a living condition, recalled those of *Stigmatomma pallipes* described in a former paper ('00). As the workers are quite blind it seems probable that the species leads a subterranean life, seeking its prey in the soil or under the dead leaves. This seems also to be indicated by the depth at which these small insects were found. The very robust antennæ and the beautifully developed stridulatory apparatus, which occupies the whole of the large membrane between the postpetiolar and first gastric segment, indicate that the senses of contact-odor and hearing are highly developed and may adequately compensate for the absence of visual organs.

On the 22d of May, Mr. C. T. Brues found a solitary worker of the same *Cerapachys* under a stone at Pease Park, about two miles from the locality in which the species was first taken. That the insect is extremely rare is shown by the fact that it had not been found before during three years of careful collecting in the vicinity of Austin.

CERAPACHYS (PARASYSCIA) AUGUSTÆ, sp. nov.

*Worker* (Fig. 1).—Length 2.5–3.5 mm. Head longer than broad, marginate and broadly excised behind and produced posteroinferiorly to form two acute, somewhat divergent angles, so that the head resembles in shape that of *Eciton schmitti* Emery. These posterior angles are continued downwards on either side as a fold which meets its fellow from the opposite side on the lower posterior surface of the head. Sides of head faintly and evenly convex; eyes entirely absent; lateral carinæ well-developed; frontal carinæ high, projecting, closely approximated, extending a short distance back between the antennal foveæ and ending on either side in a distinct tooth just in front of the rather pronounced frontal depression. Mandibles triangular, curved downwards at their tips, with

distinctly crenated edges to their blades. Antennal scape somewhat more than half the length of the head exclusive of the mandibles, rapidly incrassated towards its apex, which is provided with a deep concavity on the anterior lateral surface for the insertion of the funicle; funicle 10-jointed; first joint longer than broad, almost concealed in the concavity of the scape; joints 2-9 distinctly broader than long, gradually increasing in size distally, terminal joint very large, glandiform; constituting a club which is as long as the five preceding joints of the funicle. Thorax cylindrical, fully two and one half times as long as broad, oblong when seen from above, dorsal surface flattened, mesoëpinal suture hardly indicated by a faint constriction. Posterior surface of epinotum abruptly declivous, carinate on either side and with an indistinct tooth above. Petiole subcuboidal, a little longer than broad, with flat dorsal surface; lower surface produced anteriorly into a large, compressed, plowshare-like tooth. Postpetiole flattened dorsally, one and a half times as long as the petiole; when seen from above its anterior margin is hardly broader than the petiole, but its posterior border is half again as wide; its lower surface is convex and projects forward a little in front of the anterior dorsal border. Stridu-

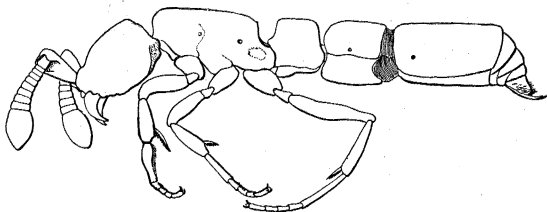


FIG. 1. *Cerapachys (Parasyscia) augustæ* n. sp. Worker.

latory organ highly developed, occupying the whole of the intersegmental membrane between the postpetiole and gaster. First gastric segment cylindrical, flattened on its dorsal surface, fully one and a half times as long as the postpetiole, slightly wider behind than in front. Remaining gastric segments very short, forming a rapidly declivous termination to the abdomen; second, third and fourth gastric segments of about equal length, tergite of the fifth segment triangular, covered with small but distinct spines on its lateral and posterior border. Sting thick, exserted. Legs rather short, all the tibiae furnished with pectinate spurs.

Surface of body shining, except the head, which is subopaque. Mandibles finely and indistinctly striated. Head covered with large, close-set, umbilicate foveolæ except on the folds of the posterior angles which are coarsely coriaceous. Whole thorax covered with umbilicate foveolæ like those on the head. On the petiole and postpetiole the foveolæ are as large as those on the head and thorax but less densely aggregated; on the first gastric segment the foveolæ are distinctly smaller and much further apart.

Whole body covered with long, suberect, golden yellow hairs, which on the head, thorax and abdomen, arise from the umbilicate centers of the foveolæ. Hairs on the terminal antennal joint very short and dense, contrasting with the longer hairs on the scape and short joints of the funicle.

Color red, edges of mandibles, clypeus, anterior border and posterior angles of head, the funicle with the exception of the terminal joint, the articulations of the thorax, legs and abdomen and the tip of the latter blackish. Legs and terminal antennal joint slightly more yellowish than the remainder of the body.

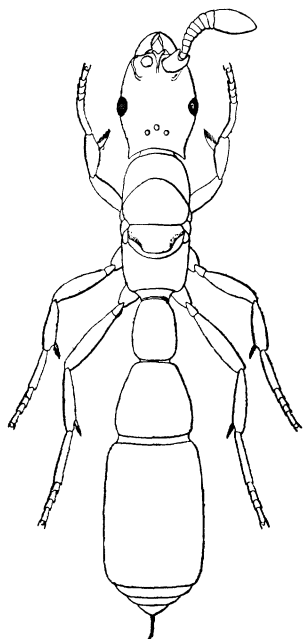


FIG. 2. *Cerapachys* (*Parasyscia*) *augustæ* n. sp. Aptерous female.

*Female* (Fig. 2).—Length 3.75 mm.

Eyes moderately large, convex, situated in the middle of the lateral surface of the head, which is shaped like that of the worker. Ocelli well developed, not lying at the corners of an equilateral, but of an isosceles triangle with a long base. Prothorax large, scutum of mesonotum well developed, dorsally flattened, without parapsidal sutures; tegulæ large, elliptical; no paraptera between the scutum and the well-developed, flattened scutellum, metanotum narrow but distinct; epinotum large, shaped like that of the worker. On the pleural surface the mesothoracic epimerite and episternum are distinct but these elements in the metapleuræ are more obscurely separated. There is nothing to show that the thorax has ever borne wings. Petiole longer than broad, postpetiole almost twice as broad as the petiole, its posterior border nearly coextensive with the edge of the first gastric

segment, which is both broader and longer than this segment in the worker. Terminal gastric segments and sting in all respects like those of the worker.

The sutures of the thoracic dorsum are blackened; otherwise the female is like the worker in coloration, sculpture and pilosity.

As *Cerapachys augustæ* has 11-jointed antennæ it must be placed in Emery's subgenus *Parasyscia*. Emery ('01<sup>a</sup> and '01<sup>b</sup>) has recently published a revision of the ants of the subgenus *Cerapachys* and the allied genera which he groups together as Cerapachyinae, a supertribal division comprising the following tribes, genera and subgenera.

*Tribe I. Acanthostichii*—with the single South American genus *Acanthostichus* Mayr.

Tribe 2. *Cerapachyi* (Africa, Asia, Australasia and Texas!).

Genus *Cerapachys* Smith (antennæ with a one-jointed club).

Subgenus *Cerapachys* (antennæ 12-jointed).

Subgenus *Parasyscia* Emery (antennæ 11-jointed).

Subgenus *Oöceræa* Roger (antennæ 10-jointed).

Subgenus *Syscia* Roger (antennæ 9-jointed; first gastric segment but little longer than the postpetiole).

Subgenus *Cysias* Emery (antennæ 9-jointed; first gastric segment much longer than the postpetiole).

Genus *Phyracaces* Emery (terminal antennal joint not forming a club—Madagascar, Africa, Borneo).

Genus *Lioponera* Mayr (2–3 terminal joints of antenna forming a club—India, Sumatra).

Genus *Sphinctomyrmex* Mayr (abdomen constricted behind each segment—Brazil).

Tribe 3. *Cylindromyrmæ*.

Genus *Cylindromyrmex* Mayr (antennæ 12-jointed; South America).

Genus *Simopone* Forel (antennæ 11-jointed; Madagascar).

The occurrence in America of a representative of the largest and most diversified genus of the Cerapachyinae is of some interest in view of the fact that this group is the most archaic and generalized of existing Formicidæ. It is, in fact, the group from which Emery and Forel would derive both the Dorylinae and Ponerinae, themselves very primitive subfamilies of ants. Inasmuch as the three remaining subfamilies (Myrmicinae, Dolichoderinae and Camponotinae) are derivable from Ponerine forms, it is evident that the Cerapachyinae must constitute a group of high phyletic significance. Emery ('95) has even gone a step further and pointed out the close resemblance of the Cerapachyi to the Mutillidæ, especially to forms like *Apterogyna*, which have a very ant-like pedicel to the abdomen and resemble the ants in many other particulars. I have copied his figure of *Apterogyna* (Fig. 5) for the sake of showing the close resemblance of this primitive Mutillid to certain species of *Cerapachys*, e. g., *C. peringueyi* (Fig. 3).

While Emery and Forel agree in regarding the Cerapachyinae as the most primitive of Formicidæ, they hold very different

opinions concerning the subfamily to which the group should be assigned. Emery ('95, '01<sup>a</sup>), who emphasizes morphological characters, regards the Cerapachyinae as veritable Dorylinae, while Forel ('99, '01), who is inclined to lay considerable stress on ethological characters, maintains that these ants are true Ponerinae. Accordingly Emery includes the Cerapachyinae and Dorylinae (*sens. str.*) as two coördinate groups under the sub-

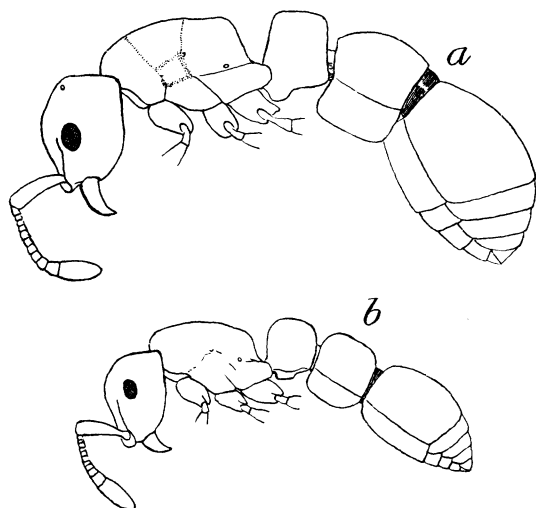


FIG. 3. *Cerapachys peringueyi* Emery. *a*, female (apterous); *b*, worker.  
After Emery.

family Dorylinae, whereas Forel would regard the three tribes Acanthostichii, Cerapachyi and Cyliandromyrmii as so many tribes of Ponerinae.

Emery's position may be stated as follows: Almost nothing is known concerning the habits of the Cerapachyinae and mere ethological inferences cannot help us in deciding the question of affinities. The female of *Acanthostichus* (see Fig. 4, *a*) is wingless and decidedly *Dichthadia*-form ("bâtie sur le type *Dichthadia* à peine mitigé"), like the females of *Dorylus* and *Eciton*. The males of the Cerapachyinae have no cerci and have retractile copulatory organs like the Dorylinae, whereas the cerci are present and the genitalia more or less exserted in the male Ponerinae. In general, comparatively little value can be attached to the con-

ditions of the pedicel in the taxonomy of ants, so that we should not emphasize the Ponerine-like petiole and postpetiole of the Cerapachyinae, especially as all sorts of pedicels are found among the different genera of this group from that of *Acanthostichus*, which is like *Amblyopone*, to that of *Oöceræa*, which recalls the conditions seen in the Myrmicinae. The larvæ of the Cera-

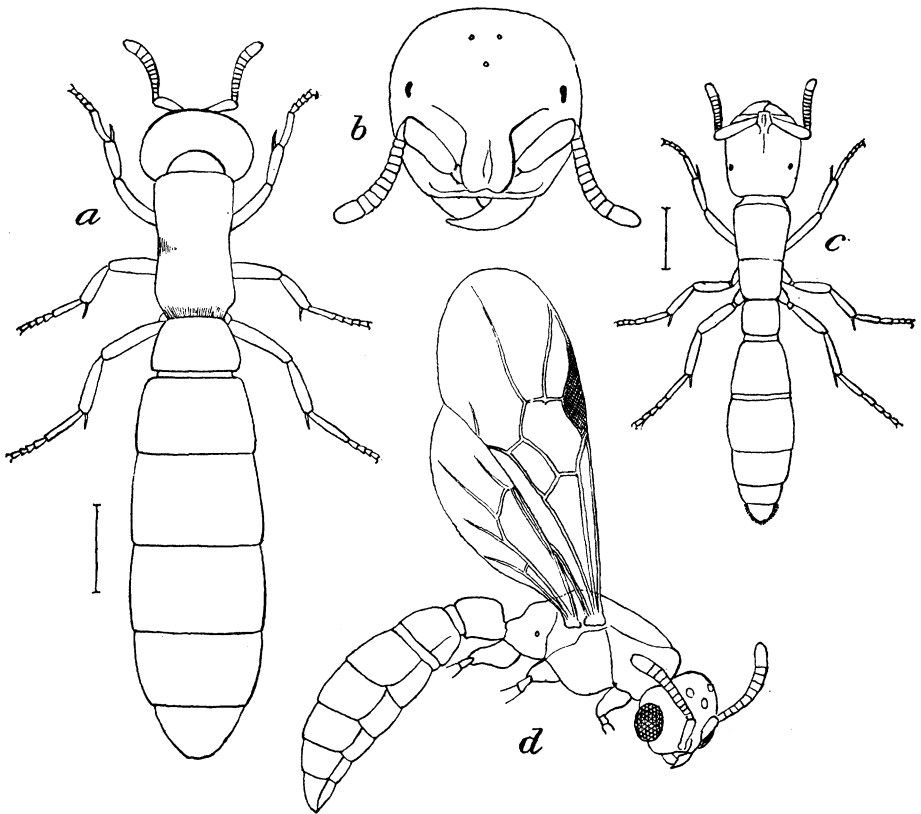


FIG. 4. *a*, *Acanthostichus quadratus*, ♀; *b*, head of same from front; *c*, large worker (same magnification as *a*); *d*, *Acanthostichus fuscipennis*, ♂. After Emery.

pachyinae are unknown, but as non-tuberculate larvæ, somewhat resembling those of *Eciton*, occur in some distinctively Ponerine genera (*Stigmatomma* and *Ectatomma*) it is probable that the larval characters would have little weight in solving the problem under consideration.



Forel, on the other hand, advances the following reasons for regarding the Cerapachyinae as true Ponerinae. While they undoubtedly exhibit traits which ally them with the Dorylinae, their habitus is, nevertheless, decidedly Ponerine. The little that is known of their habits certainly indicates that they live in small, stationary colonies like the Ponerinae, instead of populous, nomadic colonies like the Dorylinae. The queens, moreover, are so nearly of the same size as the workers as to preclude anything like the great fecundity of the queens of *Dorylus* and *Eciton*. The Cerapachyinae, too, have short legs of such a structure as to indicate a slow gait and more sedentary habits. The workers of the Cerapachyinae have ordinary faceted eyes, whereas those of the Dorylinae are absent or ocelliform, while the atrophied eyes of the Ponerinae have a very different structure.<sup>1</sup> The conditions of the

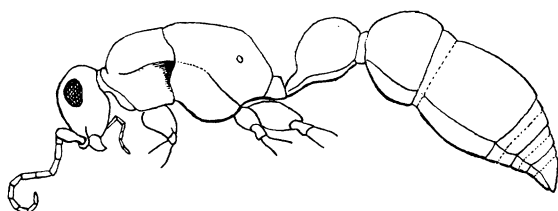


FIG. 5. *Apterogyna olivieri*. Female, after Emery.

pedicel in the males, females and workers of the Cerapachyinae are correlated as they are in the Ponerinae, and do not exhibit the differences seen in the Dorylinae between the worker on the one hand and the male and female on the other. The wingless con-

<sup>1</sup> The distinction to which Forel calls attention is worthy of histological study. I am inclined to think, however, that it may be a distinction without a difference. I have recently sectioned a number of pupæ of *Eciton schmitti* and find that the ocelliform lateral eyes are really very much atrophied compound eyes, too much atrophied, in fact, to be at all functional as visual organs. *The retinal hypodermis, which is somewhat thickened under the convex lens, shows indistinct but unmistakable traces of ommatidia. The optic nerve is very short and not connected with the brain. It ends freely in a blunt point a short distance from the ommatidial layer. This is interesting as proving that the visual fibers must arise in the retina and grow towards the brain and not in the reverse direction from cells in that portion of the brain known as the optic ganglion.* If there is a distinction between the abortive eyes of the Dorylinae and Ponerinae it would seem to be that in the former subfamily the ommatidia disappear both by fusion with one another and by reduction in number, while in the latter the number of ommatidia is gradually reduced without fusion.

dition of the female Dorylinæ is not of so much value in view of the fact that some true Ponerinæ (*Leptogenys*, *e. g.*) have wingless ergatoid queens. The characters drawn from the male genitalia are not of themselves sufficiently important to determine the allocation of the Cerapachyinæ in a particular subfamily.

My own observations on the living *Cerapachys augustæ*, though very fragmentary, incline me to accept Forel's views and to regard the Cerapachyinæ as true Ponerinæ. There was certainly nothing in the habits of the insects to remind me of the Doryline ants notwithstanding their striking morphological resemblance, especially in the shape of the head, and the blindness of the workers, to certain species of *Eciton* (*E. schmitti* Emery, *E. sumichrasti* Norton, *E. wheeleri* Emery). The small colony, with its queen so like the workers in size and structure, and the slow movements of the insects, all very closely resemble the conditions found in many lowly organized Ponerinæ, *e. g.*, *Stigmatomma*, and I may add also, *Proceratium* and *Sysphincta* to judge from the account (*in litteris*) of my friend, Rev. P. J. Schmitt, O.S.B., who has been so fortunate as to observe living colonies of these rare ants. Moreover, the fact that specimens of Cerapachyinæ are rare in collections would seem to show that the nests of these insects are not at all populous. It is safe to say that if *C. augustæ* were like the timid *Ecitons* in its habits, it would have been impossible to find a remnant of the colony on the day following the ransacking of the nest. Morphologically the Ponerinæ are certainly a very heterogeneous assemblage of forms, but this is merely what we should expect to find in so ancient and extensive a group. The addition of the tribes of the Cerapachyinæ to this subfamily would increase but little the already existing heterogeneity, since these ants are closely related to forms like *Proceratium* and *Sysphincta* which Emery formerly regarded as Dorylinæ but has since placed with the Ponerinæ. When the Cerapachyinæ are included with the Ponerinæ, the Dorylinæ become a more homogeneous subfamily, while the Ponerinæ represent the diversified and often peculiarly specialized survivors of the ancient stock from which all the other subfamilies of ants have been descended.

It is an interesting and probably significant fact that all the

various forms of females to be met with among the Formicidæ are already foreshadowed in the small and very primitive group of the Cerapachyinae. Though we have no knowledge of the females of several of the genera, we may recognize no less than four different female forms:

1. The female of *Acanthostichus*, which, as Emery has shown ('95), is decidedly *Dichthadia*-like, *i. e.*, unmistakably like the huge blind and wingless females of *Dorylus* and *Eciton*. This female is considerably larger than the largest workers of the colony as shown in Emery's figures of *A. quadratus* which I have reproduced in outline (Fig. 4, *a*, *b* and *c*).

2. Normal winged females like those of most genera of Formicidæ but more similar to the workers in size and structure. These females are known to occur in the genera *Lioponera*, *Cerapachys* and *Sphinctomyrmex*.

3. The female of *Cerapachys peringueyi* from South Africa (Fig. 3, *a*). According to Emery ('95) this form is wingless and not much larger than the worker (Fig. 3, *b*), which it closely resembles in structure. It may be designated as an ergatoid female and is not unlike the ergatoids occasionally found in species of *Ponera* (*P. coarctata*, *P. opaciceps*, etc.).

4. The female represented by the above described *Cerapachys augustæ* from Texas. This form is wingless but in thoracic structure resembles the winged females of the Ponerinae in general. It is but little larger than the largest workers though possessing well-developed eyes and ocelli.

This "morphological restlessness" in the structure of the females of so small a group of genera as the Cerapachyinae is, perhaps, significant as the phyletic source to which the different female forms of all the subfamilies of ants are to be traced. We may look upon the *Dichthadia*-like queens of the Dorylinae as a further development of the conditions exhibited by *Acanthostichus*, and the ergatoids, which crop out sporadically among the Ponerinae and the higher subfamilies, may, perhaps, be regarded as cases of reversion to females of the type of *Cerapachys peringueyi* and the Mutillidæ (*Apterogyna*, *e. g.*). The pseudogynic forms of the more specialized ants (*Formica*, *Camponotus*) resemble the female of *C. augustæ*. Finally, the winged females

of *Lioponera*, *Sphinctomyrmex*, etc., like the normal winged females of the majority of the Ponerinæ, lead very naturally to the conditions seen in the more modified winged females of the Myrmicinae, Dolichoderinae and Camponotinae.

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